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NEW SERIES, NO. 61

***Hoplomyzon sexpapilostoma*, a New Species of Venezuelan Catfish (Pisces: Aspredinidae), with Comments on the Hoplomyzontini**

Donald C. Taphorn

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Murra, J. 1946. The historic tribes of Ecuador, pp. 785-821. In Steward, J. H., ed., *Handbook of South American Indians*. Vol. 2, The Andean Civilizations. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.
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***Hoplomyzon sexpapilostoma*, a New Species of Venezuelan Catfish (Pisces: Aspredinidae), with Comments on the Hoplomyzontini**

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Hoplomyzon sexpapilostoma, a New Species of Venezuelan Catfish (Pisces: Aspredinidae), with Comments on the Hoplomyzontini

Abstract

A new species of aspredinid catfish belonging to the tribe Hoplomyzontini was collected as part of a general inventory of the fishes of the Apure River Drainage (Orinoco Basin) of western Venezuela. *Hoplomyzon sexpapilostoma*, new species, is distinguished from all known aspredinids by the following combination of characters: (1) The anterior border of the snout is slightly emarginate, vs. deeply emarginate in *H. papillatus* or straight in *H. atrizona*. (2) There are no barbels at the rictus of the mouth as in *H. atrizona*. (3) They have four papillae on the upper lip, instead of three as in *H. papillatus* (or five, including the rictal pair). (4) Dorsal rays i5 vs. i6 in *H. atrizona*, i3i in *H. papillatus*. (5) Maxillary barbels long but not surpassing the pectoral fin origins (18.8% SL). (6) The ossified lateral line tubules are arranged in a zigzag pattern to a point beneath the center of the dorsal fin base, but are straight from there back to the caudal peduncle (in *H. papillatus* the zigzag pattern continues to the caudal peduncle, and in *H. atrizona* it is completely straight). (7) The second pelvic ray is slightly longer than the rest (it forms a filament in *H. papillatus* and is short in *H. atrizona*). (8) The dorsal and anal fins are united to the dorsal midline of the body by membranes (united in *H. papillatus*, free in *H. atrizona*). *Hoplomyzon* is redefined to include the new species.

Resumen

Una especie nueva de bagre aspredínido de la tribu Hoplomyzontini, *Hoplomyzon sexpapilostoma*, especie nueva, fue colectado durante un inventario general de los peces de la cuenca del Río

Apure (Cuenca Río Orinoco) de Venezuela occidental. Se distingue de las otras especies del género (*H. atrizona* y *H. papillatus*), porque tiene la siguiente combinación de caracteres: (1) El borde anterior del hocico es ligeramente bilobulado (vs. visiblemente bilobulado en *H. papillatus* y recto en *H. atrizona*). (2) No posee barbillas en el rictus como *H. atrizona*. (3) Posee cuatro papilas en el labio superior, a diferencia de *H. papillatus* que posee tres (o cinco si incluimos el par rictal). (4) Radios dorsales i5 (vs. i6 en *H. atrizona* e i3i en *H. papillatus*). (5) Las barbillas maxilares son largas pero no sobrepasan el punto de nacimiento de la aleta pectoral (18.8% de el largo estándar). (6) Los escudos de la línea lateral describen un zigzag moderado hasta un punto ubicado aproximadamente en la mitad de la aleta dorsal, pero de ahí en adelante forman una línea recta hasta el pedúnculo caudal (en *H. papillatus* se presentan en zigzag a lo largo de toda la línea lateral, y en *H. atrizona* forman una línea recta sobre toda la línea lateral). (7) El segundo radio de la aleta pélvica es ligeramente mayor que los restantes (forma un filamento en *H. papillatus* y es corto en *H. atrizona*). (8) Las aletas dorsal y anal, están unidas a la línea media del cuerpo mediante unas membranas (están unidas en *H. papillatus* y no unidas en *H. atrizona*). *Hoplomyzon* esta redefinido para incluir la especie nueva.

Introduction

Since 1978, one of us (D.C.T.) has made collections of fishes in the Apure River drainage of western Venezuela as part of a general inventory of the ichthyofauna. While working up the aspredinid material, we identified two new records for

TABLE 1. Comparison of mensural characters for the type specimens of the three species of *Hoplomyzon* and ten paratypes of *H. sexpapilostoma* (as thousandths of SL).

Character	<i>H.</i> <i>atrizona</i> *	<i>H.</i> <i>papillatus</i> *	<i>H. papilostoma</i>			
	CAS	FMNH	MCNG	Paratypes†		
	36495	94908	18669	Min.	Max.	Mean
Standard length, mm	24.0	16.9	22.7	16.3	32.0	22.7
Body depth	142	136	132	96	153	125
Predorsal length	400	408	414	382	434	410
Dorsal fin height	179	147	181	148	245	195
Caudal peduncle length	250	254	303	275	310	296
Caudal peduncle depth	42	47	35	27	40	32
Caudal fin length	—	207	189	165	227	196
Pre-anal fin length	529	527	509	495	569	528
Anal fin base length	225	224	145	104	209	157
Anal fin height	200	154	215	226	280	252
Pre-pelvic fin length	300	325	290	287	346	322
Pelvic fin length	221	183	167	153	203	170
Pelvic fin interspace	83	83	68	70	137	86
Pectoral spine length	212	189	156	159	216	187
Anterior branched pectoral ray length	246	195	150	160	184	168
Posterior cleithral process length	125	101	62	31	85	55
Posterior coracoid process length	108	89	99	63	103	81
Dorsomedian head length	263	272	246	231	288	260
Width between pectoral insertions	296	237	227	184	234	208
Head depth at occiput	138	136	107	106	134	119
Snout length	108	107	99	12	30	19
Eye diameter	25	12	18	11	20	14
Interorbital width	75	95	55	65	100	79
Width between anterior nostrils	67	83	46	35	61	52
Mouth width	79	83	73	61	86	74
Barbel lengths						
Maxillary	195	130	198	152	211	182
Lateral mental	92	71	46	34	69	59
Medial mental	50	41	40	26	52	41

* From Stewart (1985).

† Based on MCNG 5376 (6), MCNG 6439 (2), and MCNG 18741 (2).

the genus *Xiliphius*, tentatively identified as *X. lepturus* and *X. melanopterus*; three species of *Bunocephalus*, including possibly two new species; *Ernstichthys anduzei*; and the new species of *Hoplomyzon* described herein.

Methods

Counts, measurements and terminology follow Stewart (1985).

As part of a review of the family Aspredinidae in Venezuela, we have prepared cleared, alizarin-stained skeletons of *Xiliphius* cf. *lepturus*, *Ernstichthys anduzei*, and *Bunocephalus amaurus*. These were compared with seven similarly prepared skeletons of *H. sexpapilostoma*.

Abbreviations for institutions are: Field Museum of Natural History, Chicago, FMNH; Florida Natural History Museum, Gainesville, UF; Museo de Biología, Universidad Central de Venezuela, MBUCV; Museo de Ciencias Naturales de Guanare, MCNG; Museu de Zoologia da Universidade de São Paulo, São Paulo, MZUSP; Swedish Museum of Natural History, Stockholm, NRM; Zoologisch Museum Amsterdam, ZMA; California Academy of Sciences, CAS.

Hoplomyzon Myers, 1942

Hoplomyzon Myers, 1942, pp. 94–95; *Hoplomyzon atrizona* Myers, 1942, type species by original designation. Stewart, 1985, p. 5 (redefinition).

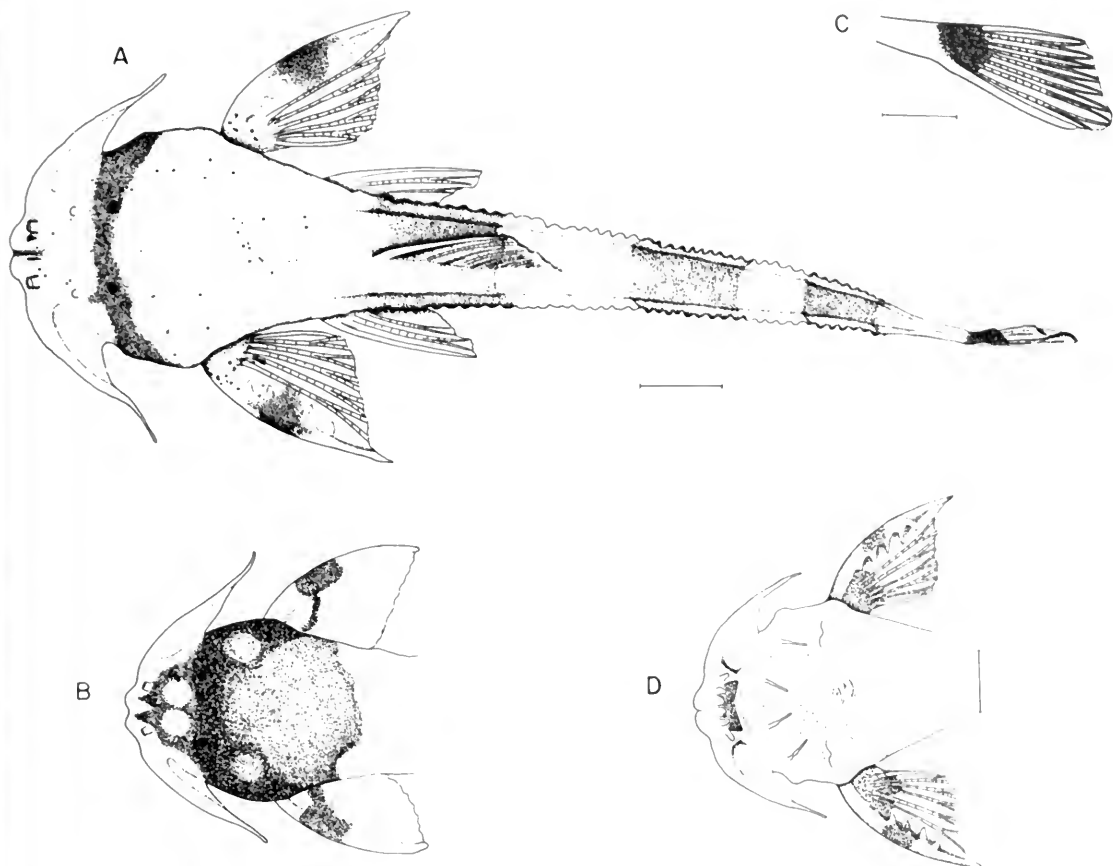


FIG. 1. *Hoplomyzon sexpapilostoma*. A, Most common color pattern (holotype). B, Color pattern of large adults, in this case a male (MCNG 18741). C, Caudal fin blotch, lateral view (holotype). D, Ventral view of the anterior part of *Hoplomyzon sexpapilostoma* (holotype). Scale bars are 2 mm.

DIAGNOSIS—(Stewart, 1985, modified to include new species.) Distinguished from all known aspredinids by having four or five stout, fleshy papillae on upper lip. Differs further from other genera of *Hoplomyzontini* in having 9 or 11 pre-anal fin plates, with three or four “paired elements”; the pectoral spine length (excluding flexible tip) less than 25% standard length; and relatively short posterior cleithral and coracoid processes; resembles *Dupouyichthys*, but differs from *Ernstichthys* in having relatively deeper caudal peduncle, greater width between anterior nostrils, and wider interorbital (table 1).

Key to Species of *Hoplomyzon* Myers

1a. Dorsal rays i3i; upper lip with three stout, fleshy papillae plus one at each rictus of mouth

for a total of five; rictal barbels lacking; ossified lateral-line tubules arranged in a zigzag pattern from near opercle to base of caudal fin ... *Hoplomyzon papillatus* Stewart, 1985

- 1b. Dorsal rays i5 or i6; upper lip with four stout, fleshy papillae plus either a slender barbel or a stout fleshy papilla at each rictus for a total of six; ossified lateral-line tubules arranged in a straight line or zigzag to beneath dorsal fin and then continuing posteriorly in a straight line 2
- 2a. Each rictus with a slender barbel; dorsal rays i6; ossified lateral line tubules arranged in straight line *Hoplomyzon atrizona* Schultz, 1944
- 2b. Each rictus with a stout fleshy papilla; dorsal rays i5; ossified lateral-line tubules arranged in a zigzag to beneath dorsal fin
... *Hoplomyzon sexpapilostoma*, new species

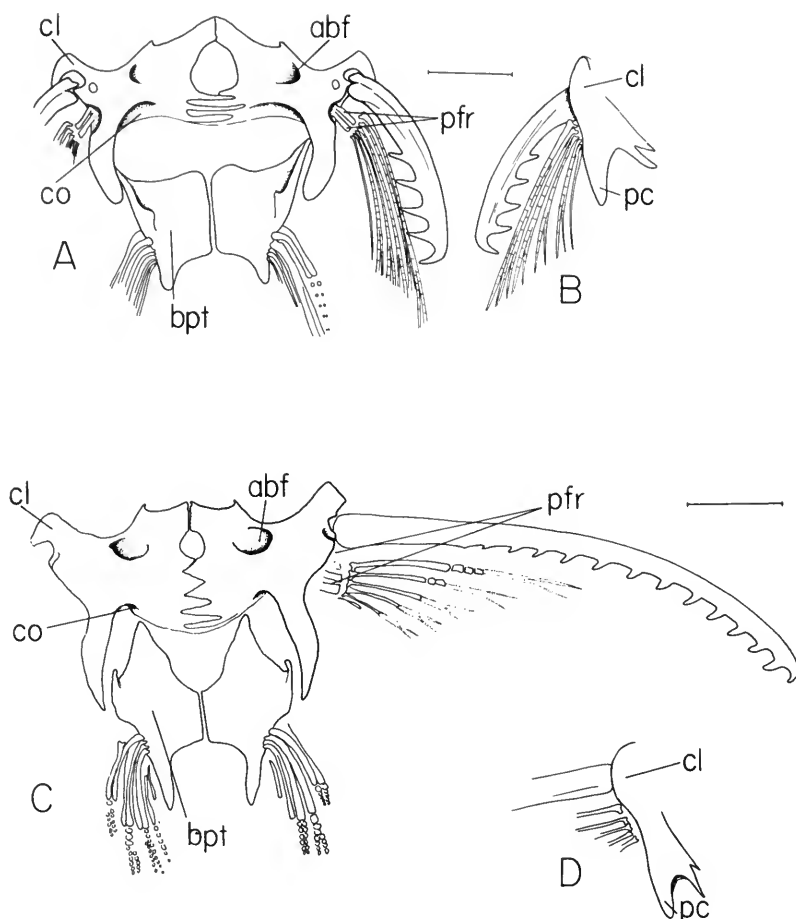


FIG. 2. A, B, *Hoplomyzon sexpapistoma* (MCNG 5376). C, D, *Ernstichthys anduzei* (MCNG 13845). E, F, *Bunocephalus amaurus* (MCNG 6038). G, H, *Xiliphius* cf. *lepturus* (MCNG 5547). A, C, E, and G show ventral views of the pectoral and pelvic girdles (with elements of right pectoral fin omitted). B, D, F, and H show dorsal views of pectoral girdle and left cleithral process. Scale bars are 2 mm. abf = abductor fossa; bpt = basipterygium; cl = cleithrum; co = coracoid; pc = posterior cleithral process; pfr = pectoral fin radials (after Schaefer, 1987).

***Hoplomyzon sexpapistoma*, new species, Figures 1–4.**

HOLOTYPE—MCNG 18669, 22.70 mm standard length, Venezuela, Barinas State, Apure River Drainage, Río Masparro at site of Masparro Dam, 70°06'00"W, 8°50'40"N, bottom rock rubble, gravel and sand with large exposed boulders. While we were fishing, the river was diverted through tunnels to expose the dam site and the reach was rapidly drying up. Specimens were collected with hand nets from the remaining puddles between 1430 and 1645 by D. Taphorn and C. Lilyestrom, 13 November 1983.

PARATYPES—MCNG 5376 (70 specimens); MZUSP 38894 (5); FMNH 97762 (5); MBUCV 17791 (7); and NRM A88/

1983457.4231 (5); all taken with holotype. Unless indicated otherwise, following lots are all from Venezuela, Portuguesa state (field numbers follow dates): MCNG 381 (6), Guanare River in La Raya, about 28 km N of Guanare, 6 June 1979, DCT79-70, D. Taphorn, C. Lilyestrom. MCNG 382 (12), Tucupido River about 2 km south of Highway 5 bridge, 27 Feb. 1979, DCT79-30, D. Taphorn, C. Lilyestrom. E. Salas, R. Feo, G. Feo. MCNG 5480 (4), border of Barinas and Portuguesa states, Bococonó River about 1 km below dam site, 5 Nov. 1982, DCT82-72, D. Taphorn, C. Lilyestrom, C. Olds, S. Reid, J. Reid, M., L. and W. Lilyestrom. MCNG 6439 (2), state of Táchira, Frio or Torbes River, about 35 km southeast of San Cristobal, 27 May 1982, DCT82-46, D. Taphorn, C. Lilyestrom, C. Olds. MCNG 8530 (4), Tucupido River at dam site, 15 Jan. 1981, DCT81-1, D. Taphorn, C. Lilyestrom, A. Fernández. MCNG 8968 (1), Tucupido River near town of Tucupido, 16 Jul. 1980, DCT80-73, D. Taphorn, C. Lilyestrom, L. Nico. MCNG 9805 (5), creek at bridge 30 km north of Guanare on road to

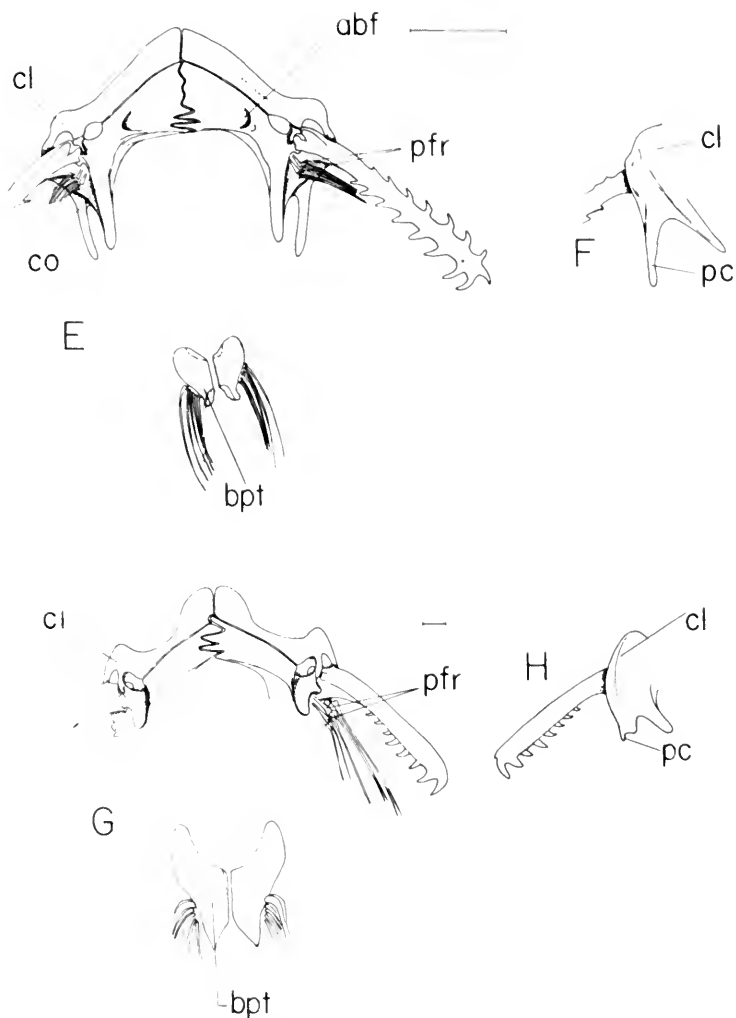


FIG. 2. Continued.

Biscucuy, 31 May 1980, DCT80-66, D. Taphorn, S. Reid, C. Staver, J. Karr. MCNG 11825 (1), Moroturo River about 15 km north of Aparición, 12 Aug. 1983, DCT83-28, D. Taphorn, C. Lilyestrom, E. Sutton, J. Sanchez. MCNG 15507 (2), Guanare River at Guanare just below dam for irrigation system, 17 Jan. 1984, KW84-2, K. Winemiller. MCNG 18741 (2), Saguas River, near bridge, in park on road to Chabasquen, 1 May 1988, ASF88-2, A. Flecker. MCNG 18905 (2), Guache River, 2 May 1988, ASF88-3, A. Flecker. MCNG 18906 (7), Barinas, Yuca River, 3 May 1988, ASF88-4, A. Flecker. MCNG 19279 (1), Boconó River below dam, 11 Jul. 1988, MC88-1, A. Barbarino. MCNG 19780 (4) Río Las Marias about 5 km NW of El Potrero, 18 Dec. 1988, ASF88-9, A. Flecker, B. Feifarek, C. Marrero, N. Camargo, M. Jiménez.

DIAGNOSIS—*Hoplomyzon sexpapilostoma* is distinguished from all known aspredinids by the following combination of characters: (1) Anterior

border of snout but slightly emarginate (figs. 1a, b, d) vs. deeply emarginate in *H. papillatus* or nearly straight in *H. atrizona*. (2) No barbels at rictus of mouth as in *H. atrizona* (fig. 1d). (3) Four papillae on upper lip (fig. 1d) instead of three as in *H. papillatus*. (4) Dorsal rays i5 vs. i6 in *H. atrizona* and i3i in *H. papillatus*. (5) Maxillary barbels long but not surpassing pectoral origins (18.8% SL). (6) Ossified lateral-line tubules arranged in zigzag pattern to point beneath the center of dorsal fin base, but straight from there back to caudal peduncle (in *H. papillatus* the zigzag pattern continues to caudal peduncle, in *H. atrizona* the line is completely straight). (7) Second pelvic ray slightly longer than other pelvic rays (it forms a filament in *H. papillatus* and is short in *H. atri-*

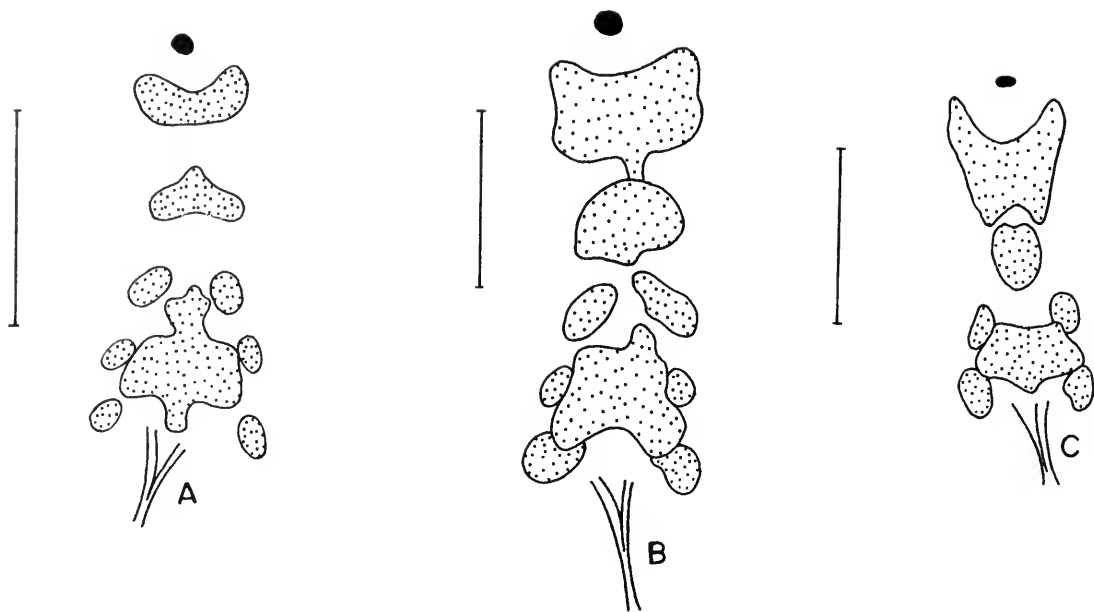


FIG. 3. Ventral elements of cleared and stained specimens. A, A 17.9 mm SL of *Hoplomyzon sexpapilostoma* (MCNG 5376). B, A 26.2 mm SL of *Hoplomyzon sexpapilostoma* (MCNG 5376). C, *Ernstichthys anduzei* (MCNG 13845). The black dots represent the anus. Scale bars are 2 mm.

zona). (8) Dorsal and anal fins united to dorsal midline of body by membranes (united in *H. papillatus*, free in *H. atrizona*).

DESCRIPTION—Mensural characters are presented in Table 1 for comparison with other species of *Hoplomyzon*. Anterior nostril on short tube, situated just behind anterior margin of snout and directed anteriorly (figs. 1a, b). Posterior nostril not very close to eye, about equidistant from anterior nostril and the eye, with lunate opening much smaller than eye diameter. Maxillary barbel supported by a bony element that extends for about one fourth of its length. Posterior coracoid processes extend far back and form lyre within which anterolateral processes of pelvic bone are included (fig. 2a). Lower caudal fin lobe longer than upper (fig. 1c).

MERISTIC DATA—Dorsal fin i5; pectoral I5i; pectoral spine with 4–5 teeth on posterior margin, anterior margin smooth (fig. 2a); flexible part of pectoral spine 31.7% of its total length; pelvics i4i, none of rays filamentous; anal fin ii5 or iii5; caudal i7i, with five rays attached to upper hypural and four to lower (this characteristic apparently unique to the *Hoplomyzontini* among all known catfishes); branchiostegal rays four; dorsal plates 21; pre-anal plates nine (figs. 3a, b); ventral plates 14; ossified lateral-line tubules 41.

PIGMENTATION—Three dark conspicuous cross-bands on dorsum—first begins at point near dorsal origin and other two cross body between the dorsal fin and tail (fig. 1a); caudal fin with dark blotch at base that covers bases of upper eight rays but does not extend onto bottom ray (fig. 1c). Females (and probably immatures of both sexes) with thin, black, masklike band that passes vertically through eyes (fig. 1a). Band is wider in some adults and whole anterior portion of head dark (fig. 1b). Pectoral spine with small black central blotch, extending onto membrane that unites spine with first branched ray (fig. 1a); spot larger and darker in males (fig. 1b). Areas between dark bands on body, anterior band through eyes, and maxillary barbels light tan. Area posterior to mask, and dorsum to just anterior to first dark band across body brown. Venter beige except where dark lateral bands continue ventrally.

DISTRIBUTION—So far found only in the Apure River drainage in Andean rivers and streams at altitudes from about 90 to 600 m. They have been found living sympatrically with *Ernstichthys anduzei* at the localities given by Stewart (1985).

COMMENTS—*Hoplomyzon sexpapilostoma* is intermediate between the two described species for some characters; however, its several unique characters, and the morphometric and meristic differ-

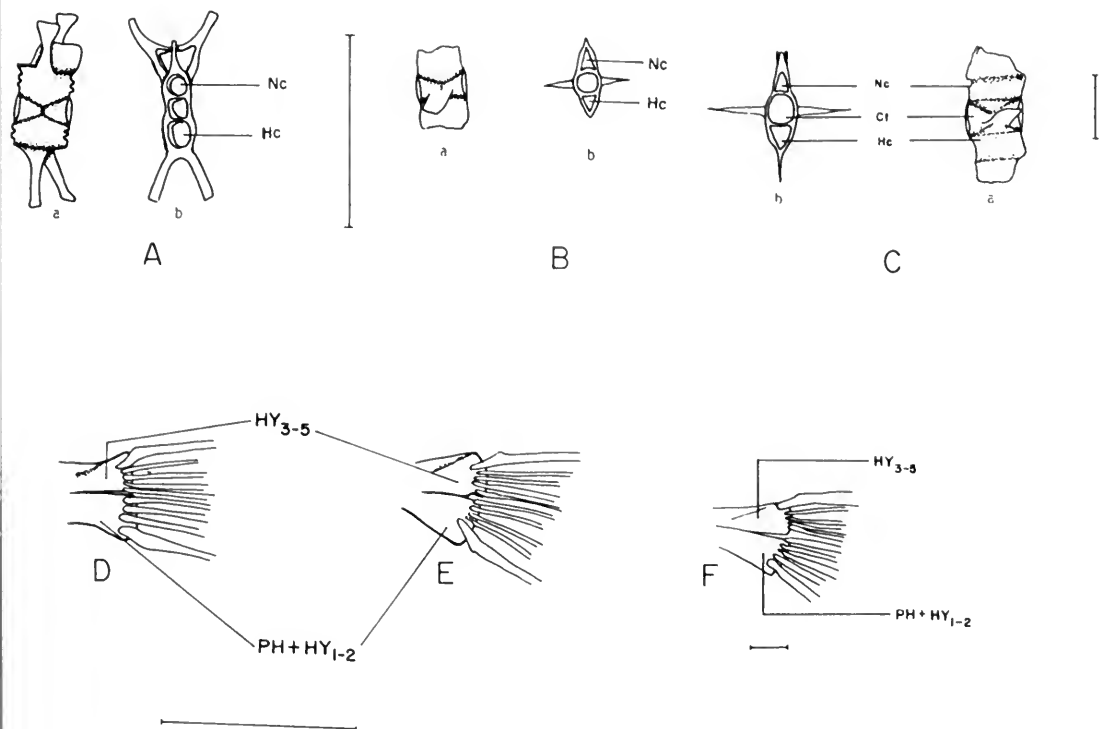


FIG. 4. Caudal vertebra in lateral (a) and frontal (b) views, and caudal skeletons. A, D, *Hoplomyzon sexpapistoma* (MCNG 5376). B, E, *Bunocephalus amaurus* (MCNG 6038). C, F, *Xiliphius* cf. *lepturus* (MCNG 5547). Ct = centrum, Hc = hemal canals, HY = hypurals, Nc = neural canals, PH = posterohyal. Scale bars are 2 mm.

ences, justify species status. We believe that the character given as typical for the genus *Hoplomyzon* by Stewart (1985), 11 preanal plates with only four paired elements, should be modified to 9 or 11 preanal plates to include *Hoplomyzon sexpapistoma*.

Comparison of the osteology of *Hoplomyzon sexpapistoma* with that of other aspredinids has revealed several important features. The so-called dermal plates along the dorsum and venter, and the "paired elements" of the belly (figs. 3a, b), are actually the expanded, flattened tips of bony struts (probably modified neural and hemal spines) that extend from the highly compressed vertebrae to the skin. They extend both dorsally and ventrally to join the vertebrae to the external plates and form a sort of X-shaped girder (fig. 4a) with two centers (the neural and hemal canals). We have found these girders in *Hoplomyzon sexpapistoma* and *Ernstichthys anduzei* but they are absent in *Bunocephalus amaurus* (fig. 4b) and *Xiliphius* cf. *lepturus* (fig. 4c).

Thus the vertebrae and struts form a solid bony connection from the top to bottom of the fish.

Opposing plates are separate from each other in front of and next to the dorsal and anal fin bases, but fuse on the dorsal and ventral midlines behind the dorsal and anal fin bases, respectively. The pairs are larger and closer to each other behind the dorsal and anal fin bases. The attachment of bifid neural spines to dermal plates in the loricariid *Hypostomus plecostomus* described by Schaefer (1987) is similar to the condition observed in *Hoplomyzon sexpapistoma*. However, *H. plecostomus* lacks bifid hemal spines, and the single hemal spines are expanded on the posterior vertebrae, not unlike the condition observed in *Bunocephalus* and *Xiliphius*.

In *Hoplomyzon sexpapistoma* (figs. 2a, b) and *Ernstichthys anduzei* (figs. 2c, d) the pelvic girdle and fins are situated between the elongated posteriorly projecting processes of the pectoral girdle (inside the "lyre"). This contrasts greatly with the condition observed in *Bunocephalus amaurus* (figs. 2e, f) and *Xiliphius* cf. *lepturus* (figs. 2g, h), in which the pelvic girdle is situated much farther posteriorly.

The greatly reduced number of caudal rays i7i,

with five attached to the dorsal hypural plate (fig. 4d), is unique among known catfishes (Lundberg & Baskin, 1969). *Bunocephalus* and *Xiliphius* have i8i with five on each hypural (figs. 4e, f).

ECOLOGY—*Hoplomyzon sexpapilostoma* typically inhabit small Andean rivers or creeks with a gravel to boulder substrate and moderate to high current. Water temperatures are usually between 24 and 28° C. Water is typically clear and flow is greatly reduced during the dry season (November–May), but flow is violent and turbidity high during the rainy season.

We speculate that their peculiar skeletal structures are an adaptation to living in the interstices of a constantly shifting substrate of gravel. These fish may have evolved structural struts that serve to protect them from being crushed when trapped inside an “avalanche” of small stones. Among the aspredinids we have examined, we have found this condition only in the Hoplomyzontini, all of which live in similar habitats. In contrast, *Xiliphius* live buried in the bottoms of larger rivers in sand or mud substrates. *Bunocephalus* are usually taken from among leaf litter in small forest streams.

This new species and all other members of the Hoplomyzontini are cryptically colored, with alternating light and dark disruptive bands. This distinct, alternating pattern is not known among other aspredinids, though all are cryptically colored to some degree.

Nothing is known about the reproduction of this species, although the females of the type series were ripe with relatively large, yellowish eggs in November (beginning of the dry season). The observed sexual dimorphism (mature males were consistently larger and had a different color pattern) suggests that some sort of courtship might be expected.

Although *H. sexpapilostoma* is small in size, and a seemingly insignificant species, it may play an important role in the trophic continuum of tropical Andean rivers. The collection of some 70 specimens when a section of the Masparro River was dried indicates that they are present in fairly high density, and that their rarity in collections is due to the usually inaccessible habitat that they occupy (we were able to collect hundreds of *Xiliphius* cf. *lepturus* under similar circumstances when a dam was closed on the neighboring Bocono River). Stomach content analyses revealed a diet of benthic macroinvertebrates, mainly aquatic insect larvae (Ephemeroptera). These insects probably shred leaves (Vannote et al., 1980) as a food source. Thus this catfish is a predator on the organisms that

capture and introduce fine particulate organic matter into the riverine foodweb.

ETYMOLOGY—From the Latin *sex* = six and *papilo* = papilla (tubercle), the Greek *stoma* = mouth. The name refers to the presence of six buccal papillae (four on upper lip, one at each corner of mouth) that distinguish the species from its congeners.

Status of the Hoplomyzontini

In the description of *Ernstichthys anduzei*, Fernández Y. (1953) recognized two families in the order Asprediformes: the Aspredidae (to include *Aspredo* and other long anal fin-based aspredinids), and the Bunocephalidae (for most other genera) and proposed the division of the Bunocephalidae into two subfamilies: Bunocephalinae for *Bunocephalus*, *Xiliphius*, *Agmus*, etc. and Hoplomizontinae for *Hoplomyzon*, *Dupouyichthys*, and *Ernstichthys*. As presently defined, the classification of these fishes is essentially the same, but Asprediformes is not used, and each subordinate level has been “demoted” one notch so that the family Aspredinidae comprises the subfamilies Aspredininae (e.g., *Aspredo*) and Bunocephalinae, with the latter subdivided into the tribes Bunocephalini (*Bunocephalus*, *Xiliphius*, etc.) and Hoplomyzontini (*Hoplomyzon*, *Ernstichthys*, and *Dupouyichthys*) as defined by Myers (1942) and Stewart (1985). Both Fernández Y. (1953) and Stewart (1985) considered the “superficial” bony plates as unique derived features that provide evidence for the monophyletic status of the Hoplomyzontini. Our observations on structure of the vertebrae, position of the pelvic girdle, the unique reduction of caudal elements, and banded pigmentation (table 2) are further evidence for monophyly of the Hoplomyzontini and widen the morphological gap that separates these tiny catfishes from other aspredinids. Further osteological analyses will probably reveal that the currently recognized genera should be regrouped into subfamilies distinct from those currently recognized. Because we lack comparative material on Aspredininae at this time, we cannot resolve phylogenetic relationships. However, based on our findings noted above, and the overall morphological similarity apparent in the few illustrations of Aspredininae available, we suggest as a working hypothesis of relationship that the Aspredininae will prove to be more closely related to the Buno-

TABLE 2. Character comparison of the tribes Hoplomyzontini and Bunocephalini.

Hoplomyzontini— <i>Hoplomyzon</i> , <i>Ernstichthys</i> , and <i>Dupouyichthys</i> (not yet seen)	Bunocephalini— <i>Bunocephalus</i> and <i>Xiliphius</i>
1) Caudal vertebrae in form of an "X."	Vertebrae in form of a cross.
2) Pelvic girdle anterior; anterior extensions of the pelvic bone included inside arch formed by posterior coracoid processes.	Pelvic girdle posterior; anterior extensions of the pelvic not included in arch formed by posterior coracoid processes.
3) Preanal plates present.	No preanal plates.
4) Principal caudal rays 5+4.	Principal caudal rays 5+5.
5) Pigmentation pattern of alternating light and dark bands.	Pigmentation uniform or mottled, not banded.
6) Dorsum and venter with series of paired dermal plates.	No dermal plates.

cephalini, sharing the characters of a posterior pelvic girdle placement and a nonbanded color pattern (although these characters may prove to be plesiomorphous once the character states have been polarized with outgroup comparisons), as well as the relatively simple cross-shaped vertebrae that lack the dorsal and ventral extensions.

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